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Effects of grass clearing and soil tilling and seasonal drought and flooding on establishment of planted tree seedlings in tropical riparian pastures

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Abstract

Anthropogenic disturbances frequently exceed resilience of riparian forests. In small-scale restoration projects revegetation is a common technique, but its success depends on the plant species used and some environmental filters. We experimentally investigated whether grass competition and soil compaction together with seasonal drought and flooding limit the establishment of seven tree species experimentally planted in abandoned riparian pastures in Southeast Mexico. We tested the effects of grass clearing and soil tilling and analyzed seasonal variation of vertical distance to water level, and changes in tree performance, microclimate, and vegetation biomass after planting. Seedling survival was low ($19\pm 3\%$), ranging between 3% (*Brosimum alicastrum*, Moraceae) and 38% (*Pachira aquatica*, Bombacaceae). Survival was negatively correlated to vertical distance to water level, highlighting the importance of the short but severe dry season that may occur in the humid tropics, which reduced survival by $>60\%$. Flooding events also produced high seedling mortality (80% after the two first events). Clearing but not tilling enhanced seedling survival. Clearing also significantly increased seedling growth of some species, suggesting competition release. Tilling did not have any consistent effect on growth, but it appears to counteract the positive effects of clearing. Both pre-existing and planted trees ameliorated microclimate to produce better conditions for establishment of new trees following natural regeneration. We conclude that clearing can enhance seedling establishment in riparian abandoned tropical pastures, but other revegetation treatments intended to reduce soil drying and uprooting by flooding during early establishment should be evaluated to improve the cost-benefit of restoring riparian forest.

Key words: Growth; Lacandona; Mexico; microclimate; restoration; survival.

1. Introduction

Riparian forests harbor high plant biodiversity (Sabo et al. 2005), support numerous ecological processes that are of key importance for multiple animals, such as fish and macroinvertebrates (Richardson et al. 2010), and provide important services for human welfare (de Souza et al. 2013). They are highly dynamic and resilient to natural disturbances, but severe anthropogenic disturbances often surpass a threshold for ~~such~~ recovery capacity (Naiman et al. 2005), leading to the degradation and loss of ecosystem services (Sweeney et al., 2004). One major anthropogenic disturbance is the conversion of forests to cropland or pastures (Naiman et al. 2005), which after some years of use are generally abandoned in a degraded condition. Restoration of degraded riparian forest in small-scale projects is mostly focused on revegetation, either relying on secondary regrowth (*i.e.*, natural regeneration or passive restoration) or active planting. For example, in streams with some level of bank stability and remnant vegetation, fencing to remove grazing may allow for passive restoration, but the post-exclusions vegetation dynamics are likely to be variable (Sarr 2002). -Some tree species may recover slowly, or not recover at all, without ~~previous~~ manipulation of the degraded riparian environment (Meli and Dirzo 2013). In such circumstances, tree planting can help to overcome the environmental “filters) that limit seed dispersal and germination (Hough-Snee et al. 2013), and which influence the final establishment of species from the regional species pool (Fattorini and Halle 2004). These filters, and hence favored species, may vary depending on the type of disturbance.

Establishment of riparian trees in abandoned cropland is often limited by light competition and ~~poor~~ soil fertility (Midoko-Iponga et al. 2005; Parsons et al. 2007; Montgomery et al. 2010; van Breugel et al. 2012). Soil compaction, resulting from forest conversion to livestock pastures (Quintana-Ascencio et al. 1996), is another potential limiting factor of tree establishment (Batey 2009). While effects of soil preparation on regeneration in traditional plantation forestry are well documented, benefits of tilling in the context of forest

restoration have been poorly assessed (Löf et al. 2012), particularly in tropical pastures.

Competition with grasses (a biotic filter) that are often exotic and soil compaction (an abiotic filter) are major limitations for tree establishment in abandoned pastures (Meli and Carrasco-Carballido 2008). The effects of these environmental filters depends on the life history and functional traits of the planted species, including seed size (Fattorini and Halle 2004; Larocheau et al. 2006), and results reported by previous scientific literature for different ecosystem types and species vary (Midoko-Iponga et al. 2005; Rey-Benayas et al. 2005; Parsons et al. 2007; Román-Dañobeytia et al. 2007; Flory and Clay 2010; García-Orth and Martínez-Ramos 2011; Löf et al. 2012; Meli and Dirzo 2013). Additionally, intense rainfall events that usually flood the stream bank and variations in soil water availability throughout the year may be also important limiting factors for tree establishment (Dressen et al. 2002).

~~Water fluctuation requires monitoring because tree species respond to variation in ground water depth (Dressen et al. 2002).~~

In this study, we used an experimental approach to investigate the survival and growth of seedlings of seven tropical rainforest native tree species that were planted into degraded riparian pastures in Chiapas, southern Mexico. We assessed the degree to which grass competition and soil compaction limited the establishment of tree species in abandoned pastures that resulted from the conversion of riparian forest into pastureland. We hypothesized that reduction of these two limiting factors would increase the overall survival and growth of planted tree seedlings and that tree survival would be related to vertical distance to water level as this variable is correlated with drought and flooding events. ~~We expected microclimate amelioration as a consequence of restoration actions and shading provided by the planted trees (Corbin and Holl 2012; Meli and Dirzo 2013).~~

2. Methods

2.1. Study site

We conducted this study in the Marqués de Comillas municipality (MdC) (16°54'N, 92°05'W) Chiapas State, Southern Mexico. MdC covers 92,242 hectares and holds 9,856 inhabitants distributed in 27 common-owned lands called *ejidos* (Inegi 2010), a communal land tenure system in Mexico. *Ejido* members have the capacity to allocate and enforce their own rights to access resources in the property.

Maximum and minimum annual temperatures are 31.8°C (April–May) and 18°C (January–February), respectively. Annual precipitation averages 3000 mm, with < 100 mm/mo from February to April and > 200 mm/mo from May to October. The primary vegetation type is lowland tropical rainforest (Dirzo 1991), attaining 40 m in canopy height in alluvial terraces along main rivers. MdC is adjacent to the Montes Azules Biosphere Reserve, which constitutes the main remnant of the Mesoamerican biodiversity hotspot, and its conservation is a nation-wide and regional priority (Myers et al. 2000). Former rainforest has been extensively converted to cattle pastures and cropland leading to a landscape mosaic of primary forest fragments, secondary forest, human settlements, and small-scale slash-and-burn agriculture and pastures (Zermeño-Hernández 2008). Deforestation also affects riparian forests, impacting both terrestrial and aquatic ecosystems (Ramírez-Martínez 2010).

2.2. Experimental design

The study was conducted in 10 riparian pastures located on the riverbank of different 2-5 m wide streams, which were spread over an area of 40 km². Pastures were abandoned 3 to 10 years after the original riparian forests were cleared and burned. These pastures were similar in structure and composition, and were dominated by the exotic grasses *Echinochloa polystachya* and *Brachiaria decumbens*. Pre-existing tree cover averaged $6 \pm 2\%$ (s.e.) per site, was absent in four sites and never exceeded 10% in any site. The associated streams with

these pastures were similar in order and geomorphology, and had a soft muddy bottom and gentle bank slopes. Annual water flow rate averages 1.37 L/s, ranging between 0.03 and 2.97 L/s. There is a typical tropical high intra-annual flow variation, which may vary between 0.21 L/s in March and 2.70 L/s in September. Our seedlings were planted in the stream floodplains and thus it is expected that their establishment is not influenced by internal hydrological characteristics of the streams such as depth or drainage density.

One plot in each of the 10 studied former pastures was established and fenced to exclude all medium-size and large herbivores, particularly the lowland paca (*Agouti paca*) and cows. Herbivory by small mammals and insects was maintained in natural and similar conditions for all planted species. Plot size had to be negotiated with land owners due to the land tenure system in the area. They were of rectangular shape, placed parallel to the stream, 8-m wide but of variable length (20 to 60 m), and their area averaged (\pm s.e.) $408 \pm 49 \text{ m}^2$ (Fig. 1). Each plot was divided into four subplots of equal size; thus, there was not intra-plot variation in subplot length within a plot but there was among plots. All subplots were parallel and from the same distance to the streams, 8-m wide, and 5-15 m long. Seedlings were planted into all four subplots and subjected to one of the following treatments: (1) no management (control treatment); (2) grass clearing; (3) soil tilling; and (4) clearing and tilling (Fig. 1). Clearing aimed at reducing competition was done by using a machete to remove above-ground grass biomass but avoid soil disturbance. A 1-m diameter circle was cleared around individual seedlings at 20-day intervals along for the two years of the experiment (Meli and Dirzo, 2013). Soil compaction, which was similar among plots before tilling (Table A.1). Tilling aimed at reducing soil compaction was done manually by the same three people in all plots, only once before tree planting, and using a hoe that disturbed topsoil to 30-cm depth. Tilling was considerably homogenous among plots. Treatments were systematically

148 applied downstream in the subplot order mentioned above in each of the 10 studied riparian
149 pastures.

150 When degradation is severe, using early-successional species has been suggested as a
151 means to accelerate vegetation recovery (Meli et al. 2013). However, besides ecological
152 criteria, other criteria related to social acceptance and technical feasibility for propagation are
153 required to optimize the identification of suitable native species for restoration, particularly in
154 rural areas where local people are involved. Therefore, we selected seven native tree species
155 based on a Species Selection Index that takes into account ecological, social, and technical
156 criteria for restoration purposes (Meli et al. 2014). We used *Brosimum alicastrum*, *Bursera*
157 *simaruba*, *Castilla elastica*, *Ficus insipida*, *Inga vera*, *Pachira aquatica* and *Vatairea*
158 *lundellii*. These species are (1) well represented in the reference ecosystem; (2) not
159 regenerating naturally; (3) show high habitat breath; (4) are socially accepted; and (5) are
160 feasibly propagated (Meli et al. 2014). They range in successional status as well (Table 1).

161 Tree seedlings were obtained from seeds that were collected in several forest
162 fragments in the region. They were grown in a local plant nursery and the initial size of
163 seedlings of the same species was homogeneous. In October of 2010, we planted a total of
164 120-200 seedlings of each species in the 10 plots. We planted them in a 1.5 x 1.5 m grid at a
165 density of 12 to 20 seedlings per species in each plot (Fig. 1), and therefore each species was
166 represented by 95-110 individuals planted in each of the four treatments. All seedlings were
167 randomly located within each subplot and all species were represented in every line of the
168 grid parallel to the stream edge.

170 2.3. Measurement of planted seedlings

171 Seedling survival, height and stem diameter were monitored 12 times on an irregular
172 basis (Parsons et al. 2007; Meli and Dirzo 2013) between October 2010 and October 2012.

We calculated the mean relative growth rate in height (RGR_{height}) and diameter (RGR_{diameter}) as $[\ln(\text{final value}) - \ln(\text{initial value})]/24$ months (Rey Benayas et al. 2005; Román Dañobeytia et al. 2012). We also estimated seedling volume as $\frac{1}{3}\pi d^2/4 \times h$ (where d corresponds to stem diameter and h to height). Height and stem diameter data were log-transformed to estimate an allometric coefficient (AC) as $\log(h)/\log(d)$, where h is height and d is stem diameter. Tree allometry is sensitive to changes in environmental factors such as the amount of solar radiation, soil fertility, and density of neighboring plants, and thus can be used as an indicator of performance of planted seedlings (García-Orth and Martínez Ramos 2011). We calculated canopy area (CA) as $[(d_1 + d_2)/2]^2\pi$, where d_1 and d_2 are the length of two perpendicular crown axes of each individual (Rey Benayas and Camacho-Cruz 2004). CA is an indicator of rain interception, light transmission and litter accumulation (Meli and Dirzo 2013). All growth variables were calculated at the end of the study.

2.4. Soil, microclimate and vegetation conditions

Plot soils were characterized by relatively low levels of organic matter, nitrogen and phosphorus, and **considerably** high bulk density (Siebe et al. 1995) (**Table A.1. in Appendix**).

We evaluated microclimate and vegetation conditions in each subplot **during one day** at the start (before planting) and **another day** at the end (two years after planting) **of the experiment. To describe microclimatic conditions**, we monitored air temperature, relative humidity (RH) and **photosynthetically** active radiation using HOBO[®] U12 model data loggers, **which were previously calibrated in a refrigerator. Temperature and RH accuracy of the sensors used were ± 0.35 °C and $\pm 2.5\%$, respectively.** Data loggers were located at the center of each subplot at 1.3 m above the ground and set to record in **30-minute increments**, resulting in 48 observations **during one day for each microclimatic variable and subplot. To describe vegetation**, we sampled grasses, broadleaf herbs, shrubs, and leaf litter in a 1-m² quadrat

located at each subplot for biomass determination. The plant mass of sampled material was quantified after drying in the lab to a constant dry weight. We also measured dbh and height of all pre-existing (October 2010) and naturally recruited trees (October 2012) (i.e., woody plants > 1.5 cm in dbh) to estimate basal area.

We did not directly quantify seasonal drought by measuring precipitation in the experimental plots. Instead, we measured water level fluctuation in the streams as a surrogate of water availability (both shortage-drought and excess-flooding) by means of buried rule bars. We buried a rule bar at the center of each plot and monitored every 15 days the vertical distance from the ground where seedlings were planted to the stream water level, or to the surface of the water column in case of flooding. Higher measured values in the rule bar represent higher distance to water level and thus shortage of water availability, whereas lower values represent flooding events.

2.5. Statistical analysis

We analyzed seedling survival at two stages of the experiment, namely (1) at the eighth month (this period included the first dry season but excluded the first flooding event), and (2) at the end of the experiment. We used a mixed model with a binomial error and a logistic link function and treated each seedling (dead or alive) as an analytical unit, instead of using averaged survival rates per species and subplot. The model included species and treatment as fixed factors, and plot was included as random factor (error). We evaluated the interactions among these explanatory factors comparing a small number of alternative models ranked according to Akaike information criteria. We also correlated mean survival by species with seed size (obtained from Martínez Ramos *et al.* unpub. data) and with vertical distance to water level across plots using Spearman rank non-parametric correlation.

Variables describing seedling growth were analyzed using a similar model as for survival analysis but with a normal error distribution. Given that we did not have surviving individuals for every species-treatment combination at the end of the experiment, we analyzed only those species with the highest survival ($n = 5$). Again, we correlated mean growth variables for each species with seed size and vertical distance to water level across plots. Growth variables (RGR_{height} , RGR_{diameter} , seedling volume, allometric coefficient, and canopy area) were highly correlated ~~between each other~~ ($r \geq 0.62$; $P \leq 0.0001$), except RGR_{height} and AC. Thus, we analyzed only these two last variables in the interest of clarity.

To assess differences in microclimate and pre-existing and newly established vegetation, we averaged each variable per treatment subplot ($n = 10$). We used MANOVA and post-hoc multiple comparisons (Bonferroni) to test for differences among the four treatments. We analyzed separately the initial condition (x_i), the final condition (x_f) and their relative change (RC) as $RC = (x_f - x_i)/x_i$. Relative humidity and light data were arcsine-square-root and log-transformed before analyses, respectively.

Survival analysis was performed with R (v3.02), whereas analyses of growth, vegetation and microclimate variables were performed with Statistica (v8; StatSoft 2004).

3. Results

3.1. Seedling survival

After two years, seedling survival for all species and treatments was quite low, and averaged $19 \pm 3\%$. Across species, survival was lowest for the late-successional species *B. alicastrum* and highest for the early-successional species *P. aquatica* and *F. insipida* (Table 1). Mean survival of all species was 29% in cleared plots and 17% in tilled plots. Only 37% and 30% of the planted seedlings survived after the first dry period (eighth month) and after the flooding events of the first year, respectively (Fig. 2).

The selected mixed models highlighted significant effects of species and treatments but not of their interaction (**Table A.2 in Appendix**). Clearing, but not tilling, had a positive effect on seedling survival (**Fig. 3 and Table A.3. in Appendix**).

Survival was not correlated with seed size across species (**Fig 4a**), but it was negatively correlated with the vertical distance to water level across plots (**Fig. 4b**).

3.2. Seedling growth

After two years, height averaged 126.9 ± 7.9 cm across the seven species and treatments (**Table 1**). RGR_{height} was lowest for the late-successional species *B. alicastrum* and highest for the mid-successional species *B. simaruba*.

Seedlings of the early-successional *F. insipida* and the mid-successional species *C. elastica* and *I. vera* grew tallest after clearing, but tilling significantly reduced growth rates (**Fig. 5a, c, d**). Seedlings of mid-successional species *V. lundelli* grew taller on untilled soils (**Fig. 5e**), whereas the early-successional *P. aquatica* did not show significant patterns in response to clearing or tilling (**Fig. 5b**). We did not analyze growth of the mid-successional species *B. simaruba* (**Fig. 5f**) and the late-successional species *B. alicastrum* (**Fig. 5g**) due to low survival (i.e. sample size).

The allometric coefficient did not show any significant difference among treatments (results not shown).

3.3. Microclimate and vegetation changes

The Relative Change Index was significantly different for all variables except for light incidence, which was similar among treatments at the start and at the end of the experiment (**Table 2**).

Some initial microclimate variables differed significantly among treatments; particularly, control and clearing showed slightly higher air temperatures, whereas clearing and tilling showed slightly lower minimum relative humidity and higher light incidence (Table 2). At the end of the experiment, air temperature differed statistically among treatments and was 1 °C higher in the tilling treatment than in the rest of the treatments. ~~At~~ The other variables did not differ among treatments.

Both initial and final measurements of vegetation did not significantly differ among treatments, in spite of the observed trend of decreasing grass and broadleaf herb biomass and increasing leaf litter biomass and tree basal area in all treatments (Table 2).

Vertical distance to water level averaged 64.1 ± 9.4 cm and varied sharply among the 10 plots. The distance ranged between 69 and 248 cm in the dry months whereas it ranged between 0 and 20 cm in the wet months. We registered four flooding events during the two years of our study, which submerged the planted seedlings > 1 m. These flooding events never lasted more than a few hours.

4. Discussion

Overall, clearing enhanced seedling performance, demonstrating that this technique facilitates the establishment of native tree species in abandoned tropical riparian pastures. These results are further evidence that competition from exotic grass and possibly pre-existing and newly established vegetation limit tree performance in tropical habitats, with high variation among species (Midoko-Iponga et al. 2005; Parsons et al. 2007; Flory and Clay 2010; van Breugel et al. 2012). However, soil tilling did not have any positive effect on the establishment of planted seedlings and the dry periods and flooding events diluted treatment effects two years after plantation took place.

4.1. Seedling survival

Clearing had significant effects on survival of four early or mid-successional species, which is in agreement with the experiments of Román Dañobeytia *et al.* (2007, 2012) in the same study region, but contrary to the results reported by Meli and Dirzo (2013) in another tropical humid forest in Mexico. This result may be due to the presence of pre-existing trees in some plots, which may produce complex interactions with the planted trees. The pre-existing trees may have shaded some planted seedlings, reducing light availability but also ameliorating high temperatures (Valladares *et al.* 2008). Similarly, pre-existing trees may compete for water and nutrients but may also enhance microbial communities (Montgomery *et al.* 2010). Pre-existing trees in our plots were scarce, but tree density increased after two years, pointing to the need of longer-term studies.

Soil compaction does not seem to be a relevant abiotic filter that impedes tree establishment in our riparian pastures. Soil compaction may constrain root growth and thus may reduce nutrient uptake (Batey 2009), as well as soil biological diversity (Potthoff *et al.* 2005). McNabb *et al.* (2012) found that tilling increases air-filled porosity and water holding capacity, which prevents excessive drying of soil. However, tilling may reduce microbial biomass, organic matter retention and soil C and N content (Powlson *et al.* 1987), destroy natural stratification of biological activity, and alter stability of soil aggregates (Aslam *et al.* 1999). Planting native vegetation can reverse these effects after several years (Potthoff *et al.* 2005), but all these effects can potentially increase erosion of the upper soil layers (Kay 1990), reduce plant rooting and hence making planted trees more vulnerable to uprooting by flooding events. Tilling can even increase the level of compaction under certain environmental conditions (Löf *et al.* 2012, McNabb *et al.* 2012), and this could have obscured our results, considering that we could not measure soil compaction at the end of the experiment.

In our study, survival rates and seed size were not correlated, contrary to the frequently described observation. This may be due to the fact that this relationship becomes weaker with time when seed reserves are fully used (Leishman et al. 2000, but see Poorter et al. 2008) or because our sample size was very small ($n = 7$ species). However, Lahoreau et al. (2006) found that the advantage of large seeds persisted even after exhaustion of seed reserves in savanna ecosystems.

Survival was negatively correlated with vertical distance to water level, further evidence of the high relative importance of the short but intense dry period in seedling establishment (Román Dañobeytia et al. 2007). Excess water availability does not seem to be a constraint for revegetation of tropical pastures, but it is a technical limitation considering that flood events swept away several planted seedlings. Regardless, flooding may be an additional and mostly independent environmental filter from grass competition or soil compaction. Moreover, interactions between flooding and other environmental variables such as light intensity could also determine complex species-specific responses that result in differential seedling responses (Hall and Harcombe 1999). Although we used vertical distance to water level as a surrogate of climatic events that should be directly measured, it suggests that water hydrological dynamics may be relevant for restoration even in the humid tropics, where the sharp variation in annual water availability can be critical in spite of the very short dry season.

4.2. Seedling growth

Clearing enhanced growth of some species, further evidence of its importance as a restoration technique. Other studies have found different effects of this technique depending on the analyzed life-history trait (Rey Benayas et al. 2005). *Castilla elastica* and *I. vera* exhibited lower height increments in non-riparian habitats of the same region (Román

Dañobeytia et al. 2007; Meli and Carrasco-Carballido 2008; Román Dañobeytia et al. 2012), possibly because riparian habitat has more suitable soil conditions and water supply than non-riparian sites. Other studies have shown that growth in height is enhanced by clearing in mid- and late-successional species, an effect of competition release from grasses (Román Dañobeytia et al. 2007, 2012). We found a significant interaction between clearing and tilling for three species, suggesting that tilling could counteract positive effects of clearing on these species, particularly for mid-successional *V. lundelli*.

Commonly, changes in allometric relations express growth strategies of plants to varying light and soil environments (Sterck et al. 2003). Early-successional species allocate more biomass to roots under low resource availability (Román Dañobeytia et al. 2012) and therefore they tend to have lower height/diameter coefficients than mid- or late-successional species. However, in our study, the allometric coefficient did not differ among species or treatments. This lack of difference was not due to unchanging microclimate conditions as two out of three microclimate variables varied significantly after two years. Rather, it seems that our allometric coefficient may not be a good indicator of growth patterns of the studied species. However, from the riparian forest restoration perspective, the study of allometric designs is of particular interest because trees with similar height but larger crowns could provide higher shading (Meli and Dirzo 2013), litter production, and suitable perches for seed dispersers (García-Orth and Martínez-Ramos 2011).

Growth in height was not related to seed size. This is an unexpected result, considering that seedlings from large-seeded species often have a well-developed root system for accessing water and nutrients (Flory and Clay 2010) and could better tolerate both competition from grasses (Lahoreau et al. 2006) and soil compaction. Growth was not correlated with vertical distance to water level either, contrary to the results obtained for

survival rates. Simmons et al. (2012) found that it could be negatively associated with flood duration, which needs to be more accurately measured.

4.3. Microclimate and vegetation changes

The initial microclimate conditions were slightly different among treatments, possibly obscuring the effects of clearing. Microclimate was more homogenous across plots at the end than at the start of our experiment, although air temperature still differed among treatments. Thus, in accordance with our hypothesis, microclimate in our restoration was less severe at the end than at the beginning of the study. Height of four of the seven planted species were in average >1.1 m tall two years after planting. Particularly, *B. simaruba* and *F. insipida* reached a mean height >1.5 m with some individuals > 2 m tall. This suggests that these species could influence microclimatic conditions. However, if these buffering effects are a consequence of the applied restoration techniques and/or of the establishment of both planted and newly recruited trees is an open question. Trees influence microclimate prevailing in the understory, favor soil formation and promote seed rain by attracting seed dispersers, which enhance forest regeneration (Meli and Dirzo 2013). ~~Decreasing grass biomass and increasing tree dbh could be related to our observed changes in microclimate (Hough-Snee et al., 2013).~~

4.4. Implications for riparian forest restoration

Our results show that clearing is a useful technique to enhance performance of tree seedlings planted in tropical riparian pastures. However, tilling did not provide the same results (but see Yates et al. 2000; Löf et al. 2012). Further, tilling could have a negative effect if it makes seedlings more susceptible to uprooting by flooding events that are typical in tropical streams. This study highlights the influence of flooding as a major environmental filter for tree establishment, and suggests the need of further research to effectively quantify

its potential effects on the establishment of planted trees. Seedling survival was also strongly related to water availability (i.e. vertical distance to water level), emphasizing the influence of short dry periods on tree mortality (Román Dañobeytia et al. 2007) even in the humid tropics. Restoration techniques, at least during the early years of establishment of planted trees, should focus on maximizing survival in spite of the potential trade-off in terms of growth (Meli and Dirzo 2013). In addition to clearing, mulching and irrigation could help avoiding desiccation during the dry period (Athy et al. 2006) and tree shelters may provide physical protection during heavy flooding events, ameliorate microclimate and accelerate woody debris retention (Andrews et al. 2010). These are promising techniques to enhance tree establishment in tropical riparian pastures and should be evaluated in future studies. Incorporating a range of agro-ecological and agro-forestry techniques in the early phases of forest restoration should be used to overcome ecological and socioeconomic obstacles to restoring riparian forests in tropical regions (Vieira et al. 2009). The important question of the extent (width and length) of the degraded riparian vegetation that should be restored to achieve ecologically effective riparian zones remains unanswered (Quinn et al. 2004).

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Supplementary material

Appendix Soil properties in restoration plots; generalized models of survival of tree seedlings and; parameter estimates of seedling survival model.

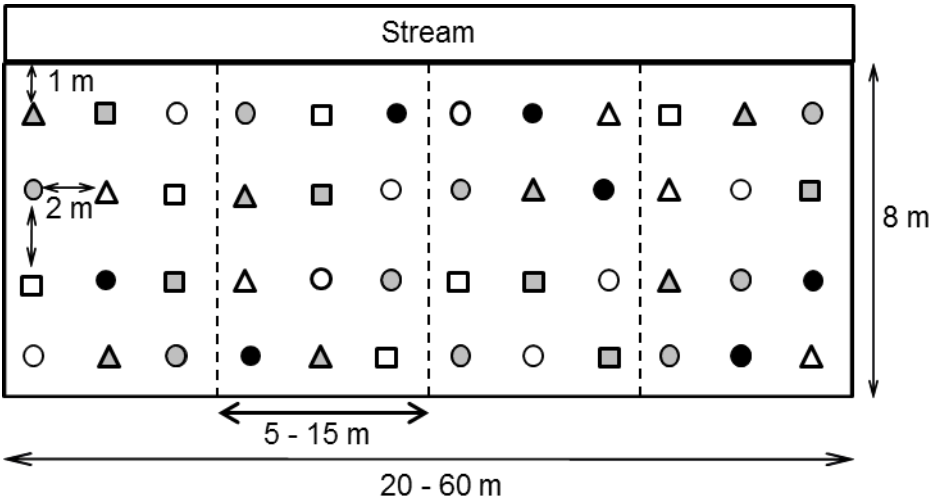


Fig. 1 Experimental design of plots in 10 tropical riparian pastures in Marqués de Comillas, Southern Mexico, and plot layout in relation to a hypothetical stream in the study area. All

plots were parallel to the streams, 8-m wide and 20-60 m long, depending on land owners' willingness. Dashed lines separate the four subplots where different treatments were applied. Position of symbols indicate the position of planted seedlings and each symbol indicates a particular species (random). See Table 1 for characteristics of seedlings and main text for treatment details.

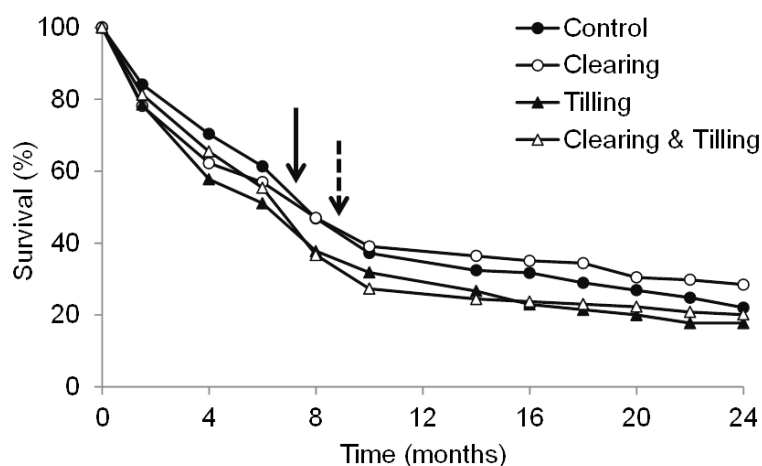


Fig. 2 Aggregated seedling survival of seven native tree species two years after planting into 10 riparian pastures under four treatment conditions. The solid arrow indicates the end of the first dry period and the dashed arrow indicates the first flooding event. Significant differences among treatments were found at eight months after planting but not at the end of the experiment.

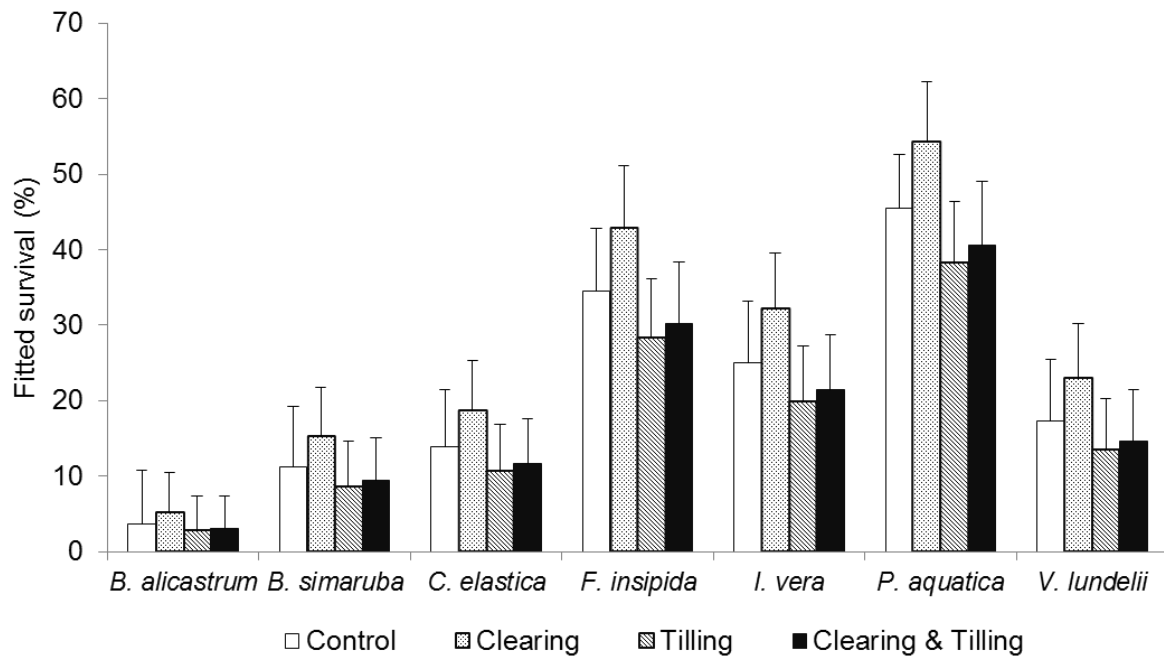


Fig. 3 Fitted seedling survival (\pm 95% confidence interval) of seven native tree species two years after planting into 10 riparian pastures under four treatment conditions. See text for details on the used model and statistical inference.

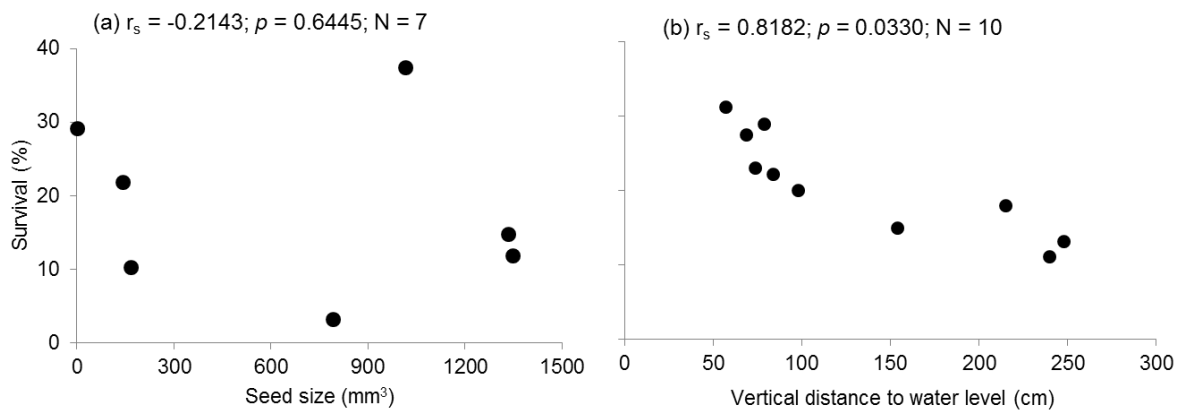


Fig. 4 Seedling survival two years after planting as a function of mean seed size (a) and vertical distance to water level (b) across seven native tree species planted into 10 riparian pastures. Spearman rank correlations are shown.

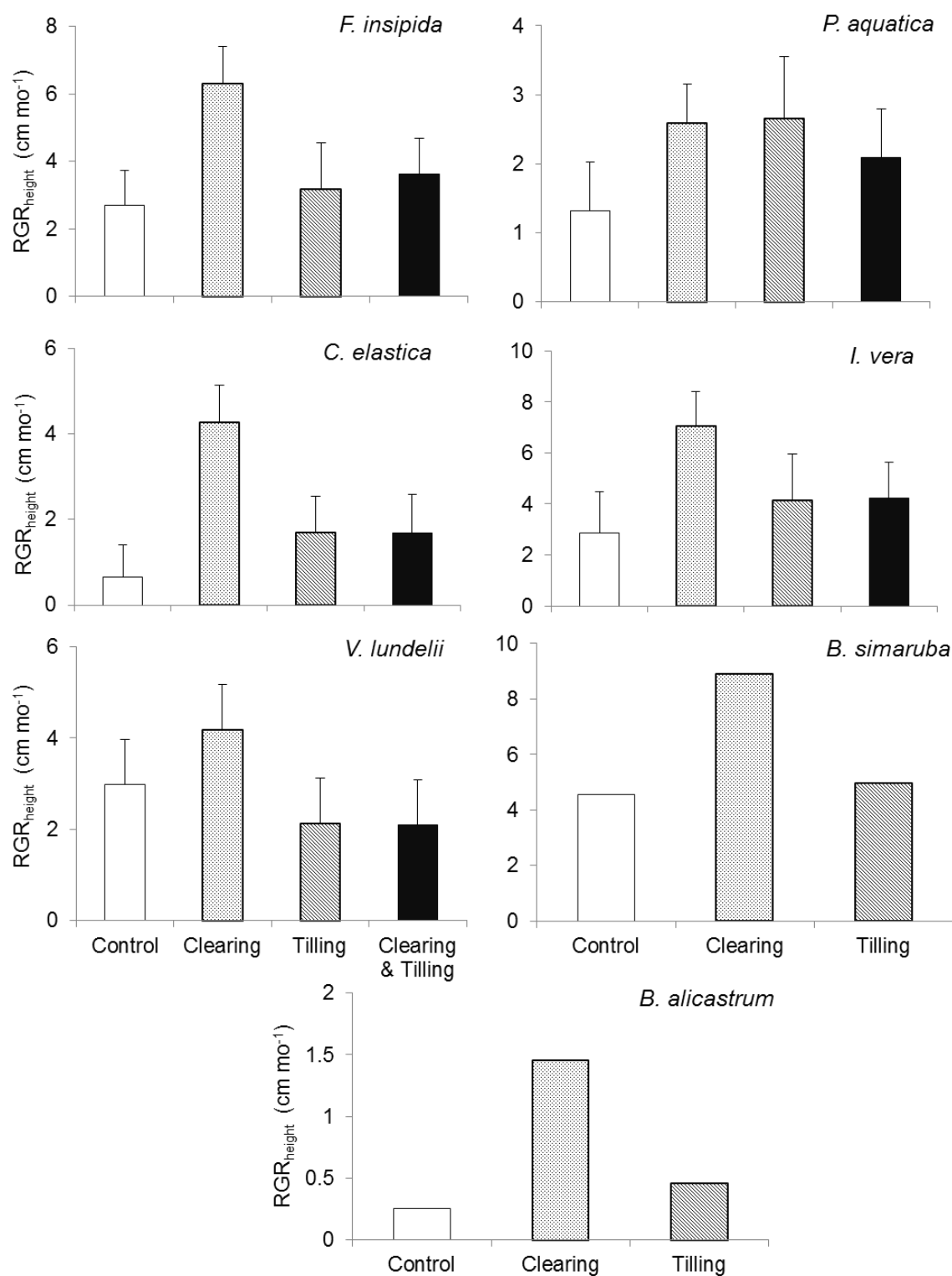


Fig. 5. Relative growth rate in height (mean \pm s.e.) of seven native tree species planted into 10 riparian pastures. Species were separately analyzed, except *B. alicastrum* and *B. simaruba* due to low sample size. * $P < 0.05$.

Table 1. Mean (\pm standard error) of characteristics of seedlings planted into 10 riparian pastures in Marqués de Comillas, southern Mexico. Two years passed between the initial and final measurements. Canopy area and allometric index (see text for formula) values correspond to surviving seedlings at the end of the experiment. Canopy area of *B. alicastrum* was not measured due to small size of the surviving individuals. Successional status categories according to Martínez-Ramos (1985). Seed volumes according to Ibarra and Oyama (1992), and Martínez-Ramos (unpublished data). All species except *P. aquatica* (anemochory) are dispersed by frugivores.

	Family	Succe- ssional status	Seed volume (mm ³)	Survival (%)	Height (cm)		RGR _{height}	Diameter (mm)		RGR _{diam}	Canopy area (cm ²)	Allometric index
					Initial	Final		Initial	Final			
<i>Brosimum alicastrum</i> Sw.	Moraceae	Late	792	3.1(1.9)	21.1(0.6)	41.3(8.3)	0.021(0.009)	2.8(0.1)	5.5(0.5)	0.048(0.001)	-	0.995
<i>Castilla elastica</i> Sesse	Moraceae	Mid	1350	11.9(3.2)	17.1(0.5)	64.2(11.9)	0.047(0.007)	2.7(0.1)	14.5(2.5)	0.043(0.003)	233.7(11.2)	0.787
<i>Bursera simaruba</i> (L.) Sarg.	Burseraceae	Mid	167	10.3(3.4)	14.5(0.6)	190.3(34.5)	0.102(0.010)	2.3(0.1)	28.5(2.5)	0.040(0.008)	66(22.5)	1.023
<i>Inga vera</i> Willd.	Fabaceae (Mimosoidea e)	Mid	143	24.5(7.8)	11.8(0.4)	137.2(22.5)	0.093(0.008)	1.2(0.04)	21.7(3.5)	0.035(0.061)	289.8(63.3)	0.847
<i>Vatairea lundelii</i> Aubl.	Fabaceae (Faboideae)	Mid	1334	17.5(8.0)	17.0(0.5)	110.8(19.8)	0.063(0.009)	3.4(0.1)	18.5(3.1)	0.045(0.002)	95.2(23.3)	1.107
<i>Ficus insipida</i> Willd.	Moraceae	Early	3.9	29.1(4.1)	28.3(1.0)	162.7(19.4)	0.061(0.007)	2.8(0.1)	32.1(4.8)	0.050(0.004)	445.7(121.9)	0.717
<i>Pachira aquatica</i> Aubl.	Bombacaceae	Early	1018.1	38.1(10.8)	47.6(2.0)	109.9(9.4)	0.024(0.003)	10.4(0.4)	28.8(2.1)	0.057(0.004)	47.0(4.5)	0.821
Total				18.8(3.3)	22.9(0.6)	126.9(7.9)	0.056(0.003)	3.7(0.1)	25.9(1.6)	0.048(0.009)	204.7(40.4)	0.880

Table 2. Mean (\pm standard error) of microclimate and vegetation variables under four treatment conditions in 10 riparian pastures at Marqués de Comillas, southern Mexico. For all variables, 48 measurements were taken every 30 minutes during one day. Figures for photosynthetically active radiation represent the daily average, whereas figures for relative humidity and temperature represent the minimum and maximum daily values, respectively. For all conditions, initial (before planting seedlings) and final (two years after) values are reported and RC indicates relative changes. See text for treatment details and statistical inference. *F* and *P* values are reported (ns, non-significant). Different letters represent significant differences at $P < 0.05$.

	Control	Clearing	Tilling	Clearing & Tilling	Average	<i>F</i>	<i>P</i>
<i>Microclimate</i>							
a) Maximum air temperature (°C)							
Initial	27.6(0.2) ^a	27.7(0.3) ^a	25.5(0.2) ^b	25.2(0.2) ^b	26.5(0.2)	23.14	<0.0001
Final	26.2(0.5) ^a	26.6(0.3) ^{ab}	27.7(0.3) ^b	26.6(0.2) ^{ab}	26.8(0.2)	3.16	0.0362
RC	-0.05(0.02) ^b	-0.04(0.02) ^b	0.09(0.02) ^a	0.06(0.03) ^a	0.01(0.02)	17.11	<0.0001
b) Minimum relative humidity (%)							
Initial	85.3(0.8) ^a	78.4(1.0) ^b	79.7(1.3) ^b	87.8(0.7) ^a	82.8(0.8)	20.30	<0.0001
Final	86.3(1.8)	86.5(1.6)	82.1(1.1)	83.5(1.2)	84.6(0.8)	2.03	ns
RC	0.01(0.02) ^a	0.10(0.01) ^b	0.03(0.02) ^{ab}	-0.05(0.01) ^{ac}	0.02(0.01)	10.21	<0.0001
c) Photosynthetically active radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$)							
Initial	569(185)	708(209)	760(227)	491(201)	636(202)	2.45	ns
Final	429(169)	523(187)	652(210)	516(179)	530(187)	1.01	ns
RC	-0.247	-0.261	-0.165	0.049	-0.166	0.53	ns
<i>Vegetation</i>							
a) Grasses (g/m^2)							
Initial	58.7(9.1)	59.6(5.5)	65.2(11.3)	71.0(6.5)	63.2(7.0)	0.74	ns
Final	39.2(9.8)	37.9(12.5)	48.4(6.6)	40.5(9.9)	41.3(9.2)	0.96	ns
RC	-0.332	-0.364	-0.258	-0.430	-0.346	1.19	ns
b) Broadleaf herbs (g/m^2)							
Initial	27.7(6.9)	15.2(4.4)	13.9(5.8)	26.0(6.8)	24.6(5.1)	2.12	ns
Final	5.9(0.9)	7.6(2.3)	7.7(3.0)	7.2(3.4)	7.2(2.5)	1.02	ns
RC	-0.787	-0.500	-0.446	-0.723	-0.707	1.18	ns
c) Shrubs (g/m^2)							
Initial	42.7(15.6)	66.3(13.3)	72.45(10.2)	27.7(13.0)	52.3(10.4)	0.40	ns
Final	48.9(10.2)	76.4(9.4)	87.5(11.1)	38.1(8.7)	62.7(11.5)	0.45	ns

RC	0.146	0.152	0.208	0.375	0.199	0.42	ns
e) Leaf litter (g/m ²)							
Initial	41.6(15.6)	51.4(11.0)	38.5(9.2)	61.1(26.2)	62.5(13.9)	1.70	ns
Final	93.4(15.6)	79.5(9.3)	60.3(11.1)	62.7(19.6)	75.5(14.5)	1.76	ns
RC	3.245	0.547	0.566	0.026	0.208	1.60	ns
d) Tree basal area (cm ²)							
Initial	17.4(7.0)	25.9(10.2)	15.9(5.4)	19.5(8.5)	19.6(8.0)	0.37	ns
Final	43.8(15.5)	48.5(12.1)	23.4(8.1)	42.2(14.6)	39.4(8.9)	0.54	ns
RC	1.517	0.873	0.472	1.164	1.010	0.10	ns

Effects of grass clearing and soil tilling on establishment of planted tree seedlings in tropical riparian pastures

New Forest

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Table A.1. Mean (standard error) of soil properties under four experimental treatments applied to 10 degraded riparian pastures at Marqués de Comillas, southern Mexico. Soil compaction was assessed by means of bulk density measured as dry soil weight per volume unit of soil collected with a metallic cylinder of 8.3 cm in diameter that penetrated 3.4 cm in the soil. One soil sample was collected at one random point in each of the four subplots. Different letters represent significant differences at $P<0.05$; (ns, non-significant).

	Control	Clearing	Tilling	Tilling & Clearing	Total	<i>F</i>	<i>P</i>
P (ppm)	3855(1369)	3047(515)	3537(648)	3532(602)	3500(413)	0.15	ns
K (ppm)	72(12)	72(13)	67(14)	71(13)	70(7)	0.03	ns
NH ₄ (ppm)	0.44(0.11)	0.38(0.07)	0.24(0.02)	0.39(0.06)	0.36(0.04)	1.29	ns
NO ³ (ppm)	1219(761)	1226(733)	1385(875)	1332(823)	1290(384)	0.01	ns
N (%)	0.17(0.02)	0.14(0.02)	0.16(0.02)	0.16(0.02)	0.16(0.01)	0.33	ns
pH	6.6(0.1)	6.6(0.2)	6.6(0.2)	6.5(0.2)	6.6(0.1)	0.19	ns
MO (%)	4.72(0.75)	4.57(0.60)	4.50(0.66)	4.94(0.58)	4.68(0.31)	0.09	ns
Bulk density (g/cm ³)	0.75(0.06)	0.69(0.06)	0.71(0.04)	0.73(0.06)	0.72(0.03)	0.19	ns

Soil temperature (°C)	35.8(1.6) ^a	45.3(2.0) ^{ab}	46.1(2.0) ^{ab}	30.5(1.1) ^b	39.7(0.9)	2.84	0.0415
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Table A.2. Generalized models of survival of tree seedlings of seven tree species 8 and 24 months after planting into 10 riparian pastures under four treatment conditions. All models included plot as a random factor. The full model included the effects of species, treatment and their interaction. The model selected based on Akaike's Information Criteria is highlighted in bold.

Model selection (backward)	No. parameter s	8 months			24 months		
		AIC	ΔAIC	Supported terms	AIC	ΔAIC	Supported terms
Full	29	772.8	0		576.9	0	
Species × Treatment removed	11	754.0	18.8	*	556.8	20.1	*
Full with only species & treatment	11	754.0	18.8	*	556.8	0.0	Supp. model
Species removed	8	755.0	-0.9	*	556.3	0.5	*
Treatment removed	5	759.9	-4.9		606.9	-50.6	
Null model (~random)	2	760.1	-0.26		604.6	2.25	

Table A.3. Parameter estimates and associated error for the supported model of seedling survival of seven native tree species planted into 10 riparian pastures. Random estimate is in the form of variance component of the model.

8 months

Fixed	Estimate	Std. Error
(Intercept)	-0.3471	0.3372
SP-BUSI	0.0649	0.3413
SP-CAEL	-0.1951	0.3434
SP-FICO	0.6675	0.3335
SP-INVE	0.4235	0.3326
SP-PAAQ	0.7844	0.3280
SP-VALU	-0.1802	0.3477
TREAT-Clear	-0.0281	0.2429
TREAT-C&T	-0.5275	0.2542
TREAT-Till	-0.4358	0.2539
Random		
(Intercept)	0.2557	0.5057

24 months

Fixed	Estimate	Std. Error
(Intercept)	-3.2772	0.6357
SP-BUSI	1.2089	0.695
SP-CAEL	1.4505	0.6743
SP-FICO	2.6391	0.6414
SP-INVE	2.1763	0.6483
SP-PAAQ	3.0947	0.6343
SP-VALU	1.7139	0.6665
TREAT-Clear	0.3514	0.2883
TREAT-C&T	-0.1962	0.3099
TREAT-Till	-0.2945	0.32
Random		
(Intercept)	0.1122	0.3349